

HEARING IN CETACEANS



BY
F. C. FRASER
AND
P. E. PURVES

PREP. 1954

Pp. 101-114 ; *Pls.* 4-5

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
ZOOLOGY

Vol. 2 No. 5

LONDON: 1954

THE BULLETIN OF THE BRITISH MUSEUM
(NATURAL HISTORY). *instituted in 1949, is
issued in five series corresponding to the Departments
of the Museum, and an Historical Series.*

*Parts appear at irregular intervals as they become
ready. Volumes will contain about three or four
hundred pages, and will not necessarily be completed
within one calendar year.*

*This paper is Vol. 2, No. 5 of the Zoological
series.*

PRINTED BY ORDER OF THE TRUSTEES OF
THE BRITISH MUSEUM

Issued January, 1954.

Price Four Shillings.

HEARING IN CETACEANS

By F. C. FRASER AND P. E. PURVES.

SYNOPSIS

Essential anatomical features of the region of the ear of cetaceans are described and figured. Earlier hypotheses relating to the mode of hearing in cetaceans are briefly reviewed and criticized.

Reasons are given for regarding the method of hearing in cetaceans as being essentially similar to that of terrestrial mammals with certain anatomical modifications required for receiving water-borne vibrations.

A simple experiment is described demonstrating the superiority of the walls of the meatus over other parts of the body as a conductor of longitudinal vibrations.

At the present time the sounds emitted by cetaceans and consequently their sense of hearing are the subject of a considerable amount of investigation. The remarks that follow are in anticipation of a more detailed account of the cetacean ear which the writers have in preparation.

In order to clarify the hypothesis arrived at a brief summary of the anatomical features involved is necessary (in connection with which reference to Plates 1 and 2 should be made).

The external auditory meatus is a continuous narrow tube in the toothed cetaceans (with the exception of *Physeter catodon*, see Clark, 1948). In the whalebone whales it is usually closed for some part of its length immediately internal to the blubber layer. The meatus is lined by a pigmented extension of the epidermis. Surrounding the lining layer is a fibro-elastic sheath, the fibres of which run predominantly along the length of the meatus. Surrounding this sheath again is a fibro-cellular structure in which a thin stratum of circular constrictor muscle has been observed.

Associated with the tube are incompletely investing cartilages into which auricular muscles are inserted. Of these one of the most important is the m. auricularis-occipitalis-profundus which Bonninghaus (1904) described and figured in detail in connection with the dissection of a Common Porpoise. Bonninghaus' figure shows the acute dorsally- and slightly caudally-directed bend into which the meatus is thrown in its course. The muscle just referred to originates at the top of the skull and extends downwards to its insertion at the apex of the bend in the meatus. Another equally important muscle is Bonninghaus' m. zygomatico-auricularis which has its origin on the zygomatic process of the squamosal and converges to be inserted into the cartilage at the inner end of the meatus.

In both toothed and whalebone whales the meatus widens out mesially to terminate at the tympanic membrane. The latter is not as in terrestrial mammals a thin translucent membrane. It consists of two parts, a fibrous region containing

radial and concentric fibres and a fibreless region similar to the pars flaccida of land mammals. The fibrous portion consists of a broad flattened triangular "ligament" with one edge of its base attached to part of the tympanic ring, the base thus forming part of the external surface of the "membrane." The attenuated apex of the "ligament" formed by the convergent radial fibres is directed mesially and is attached to a small process on the manubrium of the malleus. It is this ligament¹ which, in the opinion of the writers, is the true homologue of the fibrous portion of the tympanic membrane of land mammals. The non-fibrous portion bridges the space between the fibrous portion and the remainder of the tympanic ring. In *Phocaena phocaena* (fide Bonninghaus) the non-fibrous portion merely forms a few islets in the fibrous portion; it is single and more extensive in area in the *Globicephala melaena* specimen examined by the writers and in their opinion the "glove finger" of the whalebone whales, described by Beauregard (1891) and Lillie (1910) as well as by earlier anatomists, is the same structure very greatly enlarged.

The three auditory ossicles commonly found in the Mammalia are also represented in the Cetacea. In the latter the malleus is fixed by the processus gracilis to the margin of the tympanic annulus at the position of the Glaserian cleft. This condition is not peculiar to cetaceans, Hyrtl (1845) and Bonninghaus (1904) having described it in monkeys, carnivores and insectivores. The hammer-shape is maintained but it is the processus gracilis which resembles the handle. The head, in addition to the portion recognized as such in other mammals, includes the manubrium, which is very much reduced in length to form a short tubercle. The processus gracilis is longer and stouter than that of other mammals and in structure somewhat resembles a short length of channel girder. At the junction of the malleus with the Glaserian cleft the tympanic ring is developed into a strong wing-like lateral projection buttressed to the processus gracilis. This projection known as the sigmoid process is peculiar to the Cetacea, and plays an important part in the mechanics of the cetaceans' hearing.

The head of the malleus is deeply notched by two large facets making a re-entrant angle on its posterior aspect. Both of the facets have smooth, shallowly convex surfaces covered with articular cartilage which with the corresponding facets on the incus form part of a synovial joint. The radii of the convexities, as well as that of the arcuate junction between the two facets, lie approximately at right angles to the long axis of the tympanic ligament.

The tensor tympani muscle, which appears to be largely tendinous, is attached to the ventral wall of the periotic near that part of the tympanic cavity associated with the outlet of the Eustachian tube. Although in its course to the malleus it is directed meso-laterally approximately in line with the long axis of the tympanic ligament, the attachments of the muscle and tympanic ligament to the malleus are displaced dorso-ventrally from one another by a small distance. The ligament and muscle are not antagonistic to each other but form a mechanical couple.

The form of the incus is comparable with that of mammals generally. The facets for articulation with the malleus are shallowly concave, furnished with articular

¹ It will be referred to as the tympanic ligament in this paper.

cartilages and meet at an angle which fits into the re-entrant angle of the malleolar facets. The processus brevis is a short conical projection directed anteriorly. The ligament attaching the incus to the periotic bone, the axis of the processus brevis and the lateral margin of the processus gracilis make a common axis.

The stapes departs so little from the normal that its description is unnecessary, but it should be mentioned that, contrary to the statements which have been made that the foot is fused to the periotic at the fenestra ovalis, no evidence of this could be found by the present writers. It is probable that the impression of fusion is due to the perfect fit of the foot in the fenestra ovalis.

The tympanic bulla, the general form of which is sufficiently well known not to require detailed description, may be said to have a mesial and a lateral portion which meet ventrally in a roughly semi-circular ridge and are separated dorsally by the cavity of the bulla. The mesial part is characterized by its stout petrous nature (the bone in rorquals being up to 3-4 cm. thick), and by the smoothness of most of its surface, both of these features are associated with its contiguity with the air sinuses. The lateral portion is much thinner, and has a roughened outer surface, these features being associated with its contiguity with the surrounding fibrous layer, which is about 12 cm. thick in a large rorqual and strongly adherent to the lateral surface of the bone. The bulla in the whalebone whales is attached by two thin, flat pedicles placed respectively anteriorly and posteriorly and having their planes approximately at right angles. The cavity of the bulla is continuous with that of the middle ear and its associated air sinuses. In the *Odontocetes* the anterior pedicle is absent and the posterior support does not involve bony fusion of the tympano-periotic junction.

In all cetaceans the periotic is separated from the rest of the skull at the squamo-mastoid boundary. In the rorquals the much attenuated mastoid process is loosely wedged between the squamosal and basi-occipital bones—being maintained in position by fibrous tissue. The mastoid process of the beaked whales and some River Dolphins is less attenuated but much convoluted—the convolutions interdigitating with corresponding cavities on the postero-ventral tip of the squamosal. There is no fusion of the bones.

In the *Delphinidae* the periotic is neither wedged into, nor interdigitated with, the squamosal, but is separated from the bones of the cranium by an appreciable gap. Between the mastoid process—which is very short—and the basi-occipital there is a fibrous ligament which appears to be the only well defined point of attachment to the skull.

The cochlea and semi-circular canals occupy only a relatively small part of the petrous bone as a whole. It has been stated that in cetaceans the laminae spiralis primaria and secundaria of the cochlea make a continuous bony septum across the spiral labyrinth. The authors' dissections show that this is not so and that whilst the gap between the two laminae is very narrow at the entrance to the scalae it gradually widens towards their apex. There is a basilar membrane and organ of Corti as in other mammals. In all but absolute size the cochlea conforms with the usual pattern.

The cavity of the middle ear communicates with the Eustachian tube and with

a system of pneumatic sinuses which in volume, extent and structure are peculiar to the cetaceans.

In the region of the auditory organ accessory air sinuses occupy the space between the mesial aspect of the periotic and the surrounding bones of the skull as well as separating the periotic from soft parts on its lateral aspect.

Anterior to the tympanic bulla a very large air sinus is developed which in the porquales occupies nearly the whole of the pterygoid fossa. In the beaked whales and dolphins this sinus is even more extensive and covers the greater part of the base of the cranium in addition to the pterygoid fossa, which is very much enlarged. In the Common Dolphin this sinus has an anterior extension which passes forwards on the ventral surface of the rostrum for approximately two-thirds of the latter's length.

The mesial walls of the pneumatic sinus are closely applied to the bones of the skull. Laterally and externally the sinuses are closed by a tough, fibrous membrane resembling periosteum to which some of the muscles of the lower jaw and palate are attached. A comparative study of this membrane shows that in the more primitive species it overlies thin sheets of bone and it has been suggested that the enclosed sinuses are the homologues of the pneumatic sinuses found in the skulls of terrestrial mammals (Monro, 1785).

Within the fibrous closing membrane there is a fibro-venous plexus which extends over the whole of the inner surface of the air sinuses. The plexus is made up predominantly of large vessels which appear flattened when the sinuses are injected with air or other media but become turgid when injected themselves under pressure. In this state they obliterate the cavity of the air sinuses. Lining the latter and covering the inner aspect of the fibro-venous plexus is a thick mucous membrane which is continuous with that of the middle ear and Eustachian tube and is remarkable for the richness of its glands and ducts. The openings of the ducts, which cover the entire inner surface of the air sinuses, are less than $\cdot 1$ mm. apart and lead into a maze of smaller racemose channels and crypts lined with columnar epithelium and goblet cells.

At the entrance to the ducts and on the exposed surface of the mucous membrane is a layer of ciliated epithelium. The writers' observations, and those of Brazier Howell (1930) on freshly killed specimens reveal that the sinuses are entirely filled with an albuminous foam. Whether this is so in living animals cannot be ascertained, but the anatomical evidence suggests that it is.*

The Eustachian tube diverges from the general air cavity at a point just anterior to the tympanic bulla—and passes forwards for a short distance along the mesial aspect of that part of the sinus which goes to occupy the pterygoid fossa: thereafter it passes upwards and gradually narrowing, opens into the nasopharynx. Its closing walls are made up of fibrous tissue and a fibro-venous plexus similar to, and continuous with, that of the air sinuses. The lining mucous membrane is deeply indented with valvular pockets and folds which are directed towards the choanae.

* Additional evidence of foam in the air sinuses has been received from Mr. D. E. Sergeant, Newfoundland Fisheries Research Station, St. John's, Newfoundland, who writes (10-8-53): "*Globicephala melanaea*, female, 9' 6" in length, dead about 1½ hours. Anterior region of sinus within pterygoid exposed by means of saw cuts; seen to be filled with foam".

The fibro-venous plexus referred to above is supplied by an arterial plexus which emerges from the external maxillary artery immediately anterior to the tympanic bulla, and by small arterial branches which emerge from the same artery as it passes forwards across the ventral surface of the cranium. The plexus is drained by three distinct paths :

(1) By large vessels which communicate with the transverse and cavernous sinuses of the cranium and drain eventually into the spinal-meningeal veins.

(2) By large vessels which join the external jugular vein via the vena pterygoidea.

(3) By an intricate plexus of small veins which penetrates the fibrous covering of the sinus at the angle formed by the lateral pterygoid and the tensor palati muscles. This plexus is very dense and ramifies throughout the mass of fatty tissue which lies on the mesial aspect of the lower jaw—eventually coalescing into a single vessel which joins the external jugular vein.

The aquatic environment of whales and the extreme narrowness of their external auditory meatus have led most students of cetacean anatomy since Camper (1767) to search for some mode of hearing other than that which is normal for terrestrial mammals. Camper's hypothesis was to the effect that cetaceans could only hear when lying quietly at the surface with the external aperture of the meatus out of water. Hyrtl (1845), who recognized that whales must be able to hear well under water, held the view that while the external meatus was unsuitable for the reception of air-borne sound waves, it was suitable for the reception of " waves of compression " such as are transmitted in water.

Buchanan's (1828) belief was that sound was conducted to the tympanic membrane by way of the Eustachian tubes. This view was criticized by Claudius (1858) on the ground that the Eustachian tubes are normally closed while the cetacean is submerged. Claudius' own view was that the water-borne sound vibrations were taken up by the bones of the skull, transmitted to the pneumatic sinuses, thence to the auditory ossicles but principally to the membrane of the fenestra rotundum which he regarded as the main oscillator of the cochlear fluid. Turner (1913) agreed with Claudius' interpretation. Bonninghaus (1902) invoked the pinna-like shape of the anterior portion of the tympanic bulla as a collector of sound waves ; vibrations which he terms " molecular " are transmitted by way of the processus gracilis through the ossicles to the fenestra ovalis.

Lillie (1910) says "the whale probably receives sound vibrations by means of vibrating bony surfaces, after the manner of fishes. The tympanic bulla is a relatively dense and heavy sounding-box, fastened to the petrotic bone by two thin pedicles, so that it could easily be set in vibration. The bulla is connected with the fenestra ovalis by the chain of ossicles, the auditory apparatus being thus independent of the tympanic membrane." Kellogg (1938) concurred with this view.

In the opinion of the present writers Hyrtl's interpretation is the most acceptable one. The anatomical features of the cetacean ear, far from indicating that cetaceans hear by abnormal means, support the view that the mode of hearing is essentially

as in land mammals with precisely those modifications of structure which are required for receiving water-borne vibrations.

Any working hypothesis relating to hearing in cetaceans must be based on the assumption that these animals have the same requirements as terrestrial mammals. These requirements are that hearing should be directional, discriminative, selective and anticipative. The accepted hypotheses for directionality in hearing involve an appreciation of an intensity and/or phase difference in the sounds received by the two essential organs of hearing respectively. On the face of it it is difficult to see how this can be achieved by bone conduction.

In the binaural reception of sound necessary for directionality the advantages of the cochlea being situated at or near the extreme lateral limits of the skull are offset by the likelihood of mechanical damage and extreme limitation of voluntary controllability of the sounds entering the external opening of the meatus. The muscularly controlled pinnae of land mammals enables them, in addition to securing directionality, to control the volume of sound received. In the Cetacea the anatomical evidence indicates that binaural hearing is achieved by placing the two receptors remote from the surface of the body, by isolating them acoustically from the rest of the body and each other, and by connecting them to the surface of the body laterally by an apparently acoustically efficient muscularly-controllable vibration conduit. The acoustic isolation of the periotic is achieved by (1) its dissociation from the adjacent bones of the skull, (2) the provision and maintenance of an air gap between it and the rest of the skull at all hydrostatic pressures, (3) the foam which, on the evidence of freshly-killed animals, appears to occupy the air sacs and middle ear of the living animal. The first of these has already been described. The second is achieved by the mechanism of the accessory air sinuses. As the hydrostatic pressure increases with depth the blood is forced into the venous plexus lying below the fibrous outer covering of the sacs. The volume of the air sacs is correspondingly reduced and the compressed gas is contained in the rigid tympanic cavity and in the space between the periotic and skull. With diminishing depth the process is reversed. This interpretation of the function of the air sacs agrees with that put forward by Beauregard (1891) except that the role of the venous plexus does not coincide with his view.

Owing to the flattening of the large lining veins when the air sinuses are inflated the blood drainage from the venous plexus and mucous membrane must be predominantly through the rich plexus of small vessels which passes through the mass of adipose tissue occupying mesial concavities of the lower jaw. The very close association of the plexus with the fatty tissue and the known high nitrogen absorption capacity of the latter compared with that of blood (6 : 1) suggest that the fat may play a part in the absorption of nitrogen contained in the pneumatic sinuses. That the mucous membrane of the sinuses may have a gas-secreting function is a possibility which requires further investigation.

In considering the theory expressed by Claudius and implied by Bonninghaus that sound waves are conveyed to the tympanic bulla through the air in the pneumatic sinuses it must be pointed out that films of air surrounded by media of high acoustic resistance like water do not transmit sound well. For example, a film of .1 cm.

of air surrounded by water reflects about 93% of the incident energy of a sound wave of 1000 c.p.s. (Wood, 1941). If the air is surrounded by solid rock or presumably by a substance equally hard, for example, petrous bone, the reflected energy is about 99.93%. If in addition the air cavity is filled with foam the reduction in energy would be even greater.

The efficiency of the bubbles in damping vibrations increases rapidly both as their diameters and distance apart diminishes, thus in the cetacean as the animal dives the acoustic isolation could be maintained in spite of the reduction in volume of the foam-filled cavity.

In view of this apparent acoustic isolation of the essential organs of hearing it was decided to examine the external meatus as a possible vibration conduit. Claudius states that "All true cetaceans toothed as well as whalebone possess absolutely no functioning ear passage" and subsequently after a very incomplete description of the meatus states "The cord is then, neither homogeneous nor taut, and its conducting power very slight, and by no means any greater than that of the surrounding fat layer." The anatomical and experimental investigations carried out by the writers do not support Claudius' conclusions, but point to a set of conditions which are exactly the reverse.

The lining walls of the meatus appear extremely homogeneous (*vide supra*) and the arrangement of the two most conspicuous auricular muscles would appear to be precisely that necessary for maintaining either or both auditory conduits in any state of tension required.

In order to obtain some indication of the sound conductivity of the meatus relative to that of adjacent tissues a simple test was made. For the mechanical vibrations required the output of a variable frequency oscillator (30–10,000 c/s) was connected to the input of an amplifier of a loud speaker. A loop of dental floss was attached to the centre of the loud speaker and the two ends attached to two small pieces of perforated zinc which had been stitched to the wall of the meatus and the adjacent fibrous tissue respectively. The specimen used consisted of a large piece of the squamo-occipital region of the head of a Fin Whale which, deep frozen while fresh, had been defrosted and dissected to expose the tympanic cavity.

For indicating the relative strength of received vibration signals a gramophone pick-up was connected to an amplifier, the output of which was connected to a rectifying millivoltmeter.

With a fixed output from the oscillator and with the pick-up needle placed at the external end of the meatus, the input potentiometer of the amplifier in the pick-up circuit was adjusted to give a reading of 0.4 mv. at the millivoltmeter. To obtain the same reading with the pick-up needle placed at the malleolar end of the tympanic ligament the input potentiometer of the amplifier had to be adjusted. This adjustment corresponded to a voltage ratio of 10:1 so that assuming that the voltage reading is directly proportional to the mechanical vibration picked up, the signal received at the malleolar end was about 1/10 that applied at the outer end. When attempts were made to pick up signals on the periotic bone, on adjacent skull bones, on the muscular or on the fibrous tissue in the neighbourhood of the tympanic cavity the millivoltmeter reading fell to zero. With the apparatus available for this simple

test the limits set by the oscillator output and the amplification in the pick-up circuit, prevented a quantitative comparison being made between these last tests and the first one. The indication is, however, that the signal in any case is less than a quarter of that obtained at the malleolar end of the tympanic ligament.

The results confirmed earlier preliminary tests made with a stethoscope. Because of the mechanical difficulty of placing the stethoscope on the malleus the vibration was applied to the point of attachment of the tympanic ligament and the signal picked up at the external end of the meatus. With this arrangement good signals were received, but with the stethoscope applied to surrounding tissues results were negative.

To satisfy the discriminative condition it must be assumed that the cetacean cochlea is as selective as that of terrestrial mammals. Certainly its general anatomy suggests that this is so. The physical properties of water-borne vibrations, however, differ markedly from those which are airborne. The pressure-amplitude for the same intensity and frequency of water and air-borne sound is in the ratio $61:1$, and the displacement amplitude $1:61$. The mathematical treatment of the subject is not within the scope of this paper but it can be shown that adjustments of amplitude and pressure to values normally experienced in the cochlea by terrestrial mammals are probably achieved in cetaceans by the modifications of the malleus and incus.

Before describing the functioning of the cetacean ossicles it is necessary to repeat the often quoted *modus operandi* of the human ear. The following is from Gray's *Anatomy* (1946):

"The handle of the malleus follows all the movements of the tympanic membrane, while the malleus and incus rotate together about an axis which runs through the short process of the incus and the anterior ligament (and therefore the processus gracilis) of the malleus. When the tympanic membrane and handle of the malleus move inwards the long process of the incus also moves in the same direction and pushes the base of the stapes towards the labyrinth."

A mechanical study of their ossicles shows that the foregoing description is true for cetaceans with one important difference. In man and other terrestrial mammals the long axis of the malleus is parallel with the plane of the tympanic membrane and the manubrium is firmly attached to the latter as far as its centre. Thus the amount of movement of the centre of the tympanic membrane is identical with that of the tip of the manubrium. In cetaceans the membrane (i.e., the tympanic ligament) is attached only to a point at the tip of the manubrium of the malleus. The attachment to the tip is so situated that a line through the centre of the tympanic ligament is parallel with the long axis of the manubrium. This means that any small movement of the meatal end of the tympanic ligament produces a relatively large movement of the tip of the manubrium and therefore of the tip of the long process of the incus. In order that this amplification be produced the effective movement of the malleus must be solely rotational and this is achieved by the stout channel-girder construction of the processus gracilis and its firm fusion to the tympanic ring. In addition, its lateral edge is strongly buttressed by the sigmoid process of the tympanic ring. This construction ensures that lateral movement of the malleus is obviated and that the processus gracilis is capable of torsional vibration only. The angular articulation of the malleus with the incus produces

a condition in which there is positive oscillatory drive by rotation only. The smooth curved surfaces of the facets tend to slip over one another in one or both directions when the oscillation is transverse or longitudinal to the processus gracilis. This factor must be of great importance in the exclusion of extraneous vibrations. In this last connection it is necessary to examine the hypothesis of Lillie and Kellogg (*v. supra*) in more detail and as a preliminary it will be useful to recall Beauregard's (1894) conclusions on the subject.

"The tympanic bulla cannot be regarded as an apparatus for resonance as has been asserted by various anatomists and physiologists (Hunter, Home, Esser, etc.). The massiveness of the walls of the bulla and its shape recalling more or less that of a shell have evidently given birth to this idea, but the facts do not justify it. These so-called resonators are more or less completely enveloped by soft parts which do not favour their action. The shape is extraordinarily variable in reality and the massiveness of the walls is necessary to obtain a rapid equilibrium of pressure between the air which fills the bulla and that of the exterior. Savart was therefore correct in saying that the tympanic cavity has the function of retaining near the entrance of the labyrinth and on the internal aspect of the tympanic membrane an atmosphere of which the physical properties are constant."

In agreeing with this view the writers would draw attention to additional anatomical details which support it. (1) the great thickness and strength of attachment of the fibrous capsule which envelops the ventro-lateral aspect of the bulla, this being the part which would be most easily thrown into vibration; (2) the extreme density and thickness of that part of the bulla which is exposed to air on both surfaces, the internal damping of such a mass must be considerable; (3) the angular set of the two thin pedicles is such that the bulla would not easily be thrown into vibration, but assuming it were it would be expected to vibrate about an axis running through the pedicles. Examination of the positioning of the articular facets of the malleus in relation to this axis indicates that no drive to the incus could be achieved (the connection between the malleus and incus has already been described).

The majority of sounds in water can be regarded as being conveyed from a point source by spherical pressure waves. When such waves impinge on the cetacean body, and assuming the least favourable acoustic conditions, i.e., that the general shape and various tissues of the body are non-reflecting, the body mass would form no barrier to the progress of the waves except in the neighbourhood of the ear. Here the sound energy, except that conveyed by the external meatus, must undergo almost complete reflection because of the gaseous content of the tympanic cavity and accessory air sinuses. The walls of the external meatus would be thrown into longitudinal vibration whether or not a continuous free lumen existed. Such vibrations would be conveyed to a point on the mesial end of the manubrium mallei by the convergent fibres of the tympanic membrane. The oscillations of the malleus thus initiated would be conveyed to the cochlear fluid over the bridge formed by the auditory ossicles.

In terrestrial mammals the intensity of sounds received can be governed by orientation of the head, but principally by the use of auricular muscles. In the Cetacea the orientation of the head in relation to the rest of the body is limited by the absence of a well-defined neck. If, however, it is accepted that the sounds

received at the cochlea of the cetacean are conducted along the external auditory meatus by longitudinal waves the degree of tension of the walls of the meatus must be a controlling factor in sound intensity. The m. auricularis occipitalis profundus and the m. zygomatico-auricularis of the Porpoise described by Bonninghaus seem particularly well suited in position and structure for the function of adjusting the tension. The meatus, however, is attached to the tympanic annulus and an additional mechanism is required to maintain the tension of the fibrous portion of the tympanic membrane lying within the tympanic cavity. The positioning of the non-fibrous portion of the membrane in relation to the fibrous portion is such that under the influence of the gaseous pressure within the tympanic cavity the necessary tension could be provided. The final expression of this function can be seen in the "glove-finger" of the porpoises. In them the non-fibrous portion is enlarged in correspondence with the greatly elongated tympanic ligament.

The arrangements which exist in terrestrial mammals for making small temporary adjustments to the tension of the tympanic membrane are also present in the Cetacea, but in view of the coarse adjustment required it is doubtful whether the tensor tympani muscle is as effective in this respect as it is in terrestrial mammals. The palatal and lateral pterygoid muscles are however very well developed in cetaceans and their relationships to the Eustachian tube and pneumatic sinuses suggest that they may play an important part in the adjustment of the gaseous pressure within the tympanic cavity and consequently of the tension on the tympanic ligament.

BIBLIOGRAPHY

- BEAUREGARD, H. 1894. Recherches sur l'appareil auditif chez les Mammifères. *J. Anat., Paris*, **1894**: 367-413, 3 pls.
- BONNINGHAUS, G. 1904. Das Ohr des Zahnwales, zugleich ein Beitrag zur Theorie der Schalleitung. *Zool. Jb.*, **19**: 189-360, 28 figs., 3 pls.
- BUCHANAN, T. 1828. *Physiological Illustrations of the Organ of Hearing*. London.
- CAMPER, P. 1767. Verhandelning over het Gehoor van den Cachelot, of Pot-Walvisch. *Verh. Holland. Maatsch.*, **9** (3): 193-229, figs.
- CARTE, E., and MACALISTER, A. 1868. On the Anatomy of *Balaenoptera rostrata*. *Phil. Trans.*, **158**: 201-261, 5 pls.
- CLAUDIUS, M. 1858. *Physiologische Bemerkungen über das Gehörorgan der Cetaceen und das Labyrinth der Säugethiere*. Kiel.
- HOME, E. 1812. An Account of some Peculiarities in the Structure of the Organ of Hearing in *Balaena mysticetus* of Linnaeus. *Phil. Trans.*, **102**: 83-88, 2 pls.
- HOWELL, A. B. 1930. *Aquatic Mammals: their Adaptations to Life in the Water*. Pp. vii + 338. Springfield, Illinois.
- HUNTER, J. 1787. Observations on the Structure and Oeconomy of Whales. *Phil. Trans.*, **77**: 371-450, 8 pls.
- HYRTL, J. 1845. *Vergleichend-anatomische Untersuchungen über das innere Gehörorgan des Menschen und der Säugethiere*. Pp. viii + 139, 9 pls. Prag.
- JOHNSTON, T. B., and WHILLIS, J. (Editors). 1946. *Gray's Anatomy*, 29th ed. 1-1597, figs. London.
- KELLOGG, R. 1938. Adaptation of Structure to Function in Whales. *Publ. Carneg. Instn.*, **501**: 649-682.
- LILLIE, D. G. 1910. Observations on the Anatomy and General Biology of some members of the Larger Cetacea. *Proc. Zool. Soc. Lond.*, **1910**: 769-792, 1 pl., 10 figs.
- MONRO, A. 1785. *The Structure and Physiology of Fishes*. 1-128, 44 pls. Edinburgh.

- TURNER, W. 1914. Observations on the Auditory Organ in the Cetacea. *Proc. Roy. Soc. Edinb.*, 34 : 10-26, 4 figs.
- WOOD, A. B. 1941. *A Text-book of Sound, being an account of the Physics of Vibrations with special reference to recent theoretical and technical Developments.* 1-578, figs., tables and plates. London.

Munesato Yamada's "Contribution to the Anatomy of the Organ of Hearing of Whales," reprinted from the *Scientific Reports of the Whales Research Institute*, No. 8, 1953, was received after completion of the foregoing preliminary account. It will be considered in the more detailed paper which the authors have in preparation.

EXPLANATION OF PLATES

PLATE 4

FIG. 1.—Dissection to expose the ventral aspect of the left ear of a Pilot Whale, *Globicephala melaena*. Cut surfaces of bone hatched and the corpus cavernosum shown reflected. Abbreviations used in this and the following figures :—

AAS —Accessory air sinus.	MM —Manubrium mallei.
AC —Auricular cartilage.	oc —Occipital condyle.
AL —Anterior ligament.	P —Periotic.
AP —Anterior pedicle.	PG —Processus gracilis.
B —Blubber.	PP —Posterior pedicle.
C —Cochlea.	PTS—Pterygoid sinus.
CC —Corpus cavernosum.	S —Stapes.
EAM—External auditory meatus.	SC —Semicircular canal.
FO —Fenestra ovalis.	SM —Stapedial muscle.
FR —Fenestra rotundum.	SP —Sigmoid process.
FVP —Fibro-venous plexus.	TA —Tympanic annulus.
GL —Glove finger.	TB —Tympanic bulla.
I —Incus.	TL —Tympanic ligament.
LI —Ligamentum incudis.	TT —Tensor tympani muscle.
M —Malleus.	

FIG. 2.—Detail of figure 1.

PLATE 5

FIG. 1.—Dissection to expose the ventral aspect of the left ear of a foetal Lesser Rorqual, *Balaenoptera acutorostrata*. (Abbreviations as for Plate 4, figure 1.) Corpus cavernosum shown reflected.

FIG. 2.—Right tympanic annulus and auditory ossicles of a Humpback Whale, *Megaptera novaeangliae*. The dotted line indicates the axis of the tympanic ligament. (Abbreviations as for Plate 4, figure 1.)

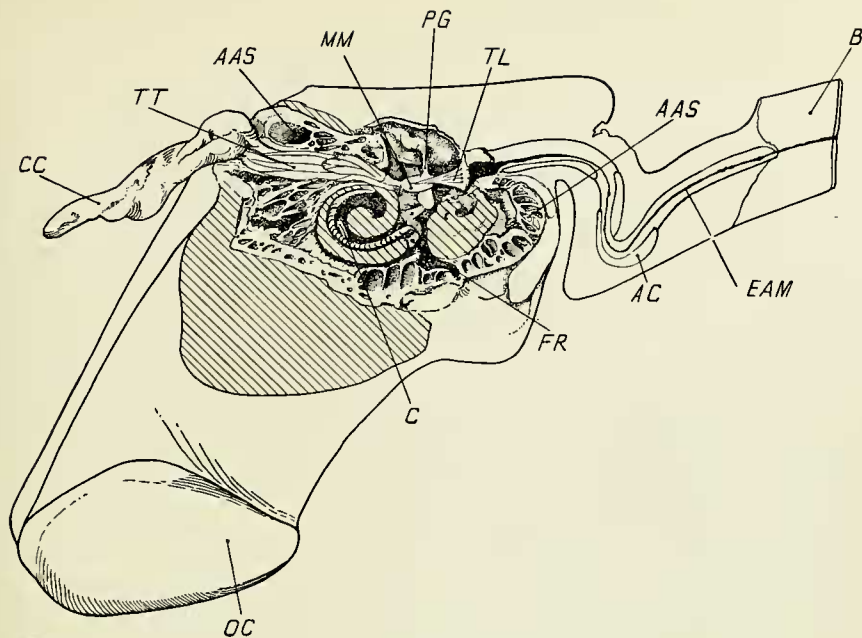


FIG. 1.

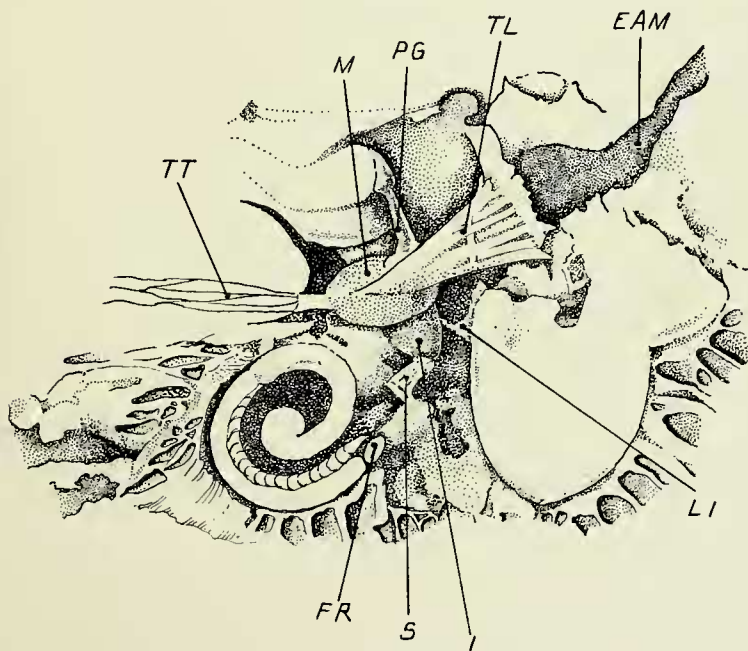


FIG. 2.

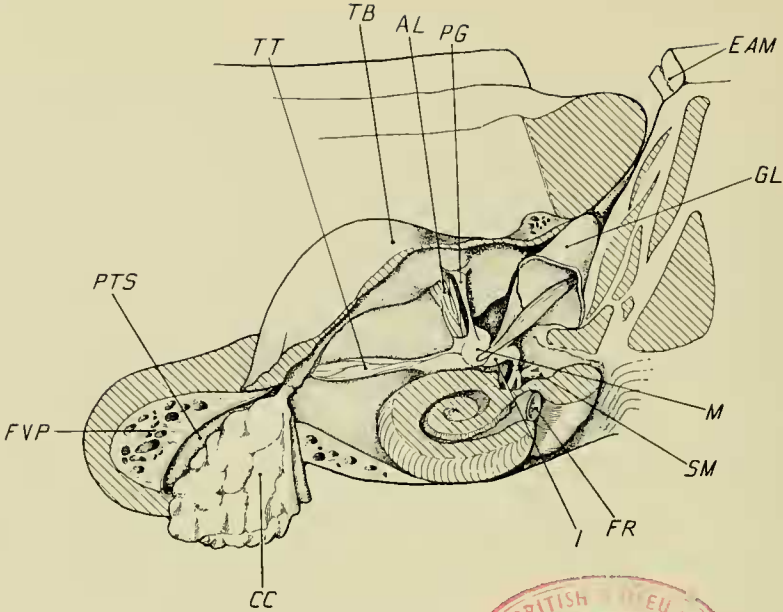


FIG. 1.

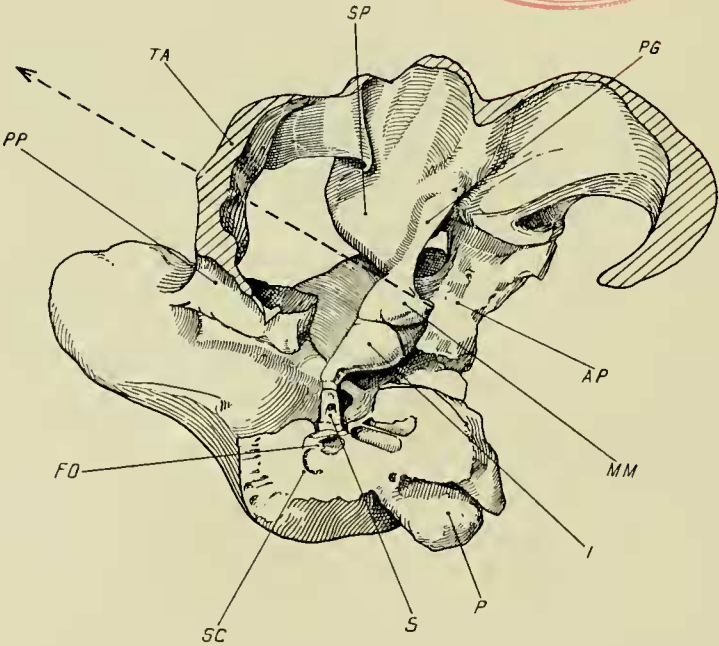


FIG. 2.